The effect of leg autotomy on terrestrial and aquatic locomotion in the wolf spider *Pardosa valens* (Araneae: Lycosidae)

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Abstract. Many species use autotomy, the self-amputation of an appendage, as a last-gasp method to escape a predator. Although this behavior can have immediate survival benefits, it can also negatively affect future survival or reproduction. The wolf spider *Pardosa valens* Barnes 1959 occurs along small mountain streams in southeastern Arizona, where it moves both on cobble along the stream and on top of the water's surface. Autotomy of legs is common in this species, and we hypothesized that such leg loss could lead to decreased sprint speed in both terrestrial and aquatic locomotion. We examined burst speed in the laboratory on artificial terrestrial and aquatic racetracks during 2005 (both males and females) and 2006 (females only). In 2005 terrestrial trials, intact spiders were faster than autotomized spiders, but there was no effect of sex on speed. In contrast, 2005 aquatic trials revealed that females ran faster than males, but that autotomy had a negative impact on the speed of females only. Additionally, female spiders generally ran faster on the terrestrial track later in the day than earlier in the day, suggesting that environmental variables such as temperature may have some influence on spider locomotion. Males were less likely to run on water than were females, and ran shorter distances when they did run. Results for females during 2006 also showed a decline in speed with autotomy, and an increase during later trials, although the results were weaker than during 2005, with only the aquatic trials showing a significant difference. These results suggest that leg autotomy in this spider does have a cost, but that the magnitude of this cost depends on aspects of the spider (e.g., sex) and habitat (e.g., substrate and environmental conditions).

Keywords: Sprint speed, performance

Many animals autotomize a body part as a defensive behavior (reviews in Maginnis 2006; Fleming et al. 2007). The body part sacrificed is typically an appendage that can be easily grasped: tails in lizards (Arnold 1988; Bateman & Fleming 2009), salamanders (Brodie 1983), and dormice (Juškaitis 2006); arms in echinoderms (Bingham et al. 2000); caudal lamellae in damselfly larvae (Robinson et al. 1991); and legs or claws in various arthropods (e.g., Carlberg 1994; Juanes & Smith 1995; Foelix 1996; Guffey 1998). Although autotomy may occur during intraspecific agonistic competition (e.g., Dodson & Beck 1993), as a response to toxins (e.g., Eisner & Camazine 1983), or during molting (e.g., Maginnis 2008), most studies suggest it results primarily from interaction with predators (Maginnis 2006; Fleming et al. 2007). Regardless of the cause, autotomy has obvious selective advantages if it allows an individual to survive an encounter that it otherwise might not.

Despite the immediate benefits, loss of the autotomized body part is not without potential future costs. One such cost arises in animals, such as lizards or echinoderms, which can regenerate the lost appendage. Regeneration diverts energy away from other processes and can lead to decreased fecundity or slower overall growth (Maginnis 2006). A second type of cost arises when lack of the body part negatively affects performance of some behavior. Individuals with an autotomized appendage may run more slowly, be more susceptible to predator attacks, be less competitive for mates, have lower prey capture success, or have lower social status than intact individuals (reviewed in Fleming et al. 2007).

A number of spiders will autotomize a leg under life-threatening circumstances (Roth & Roth 1984; Foelix 1996). For wolf spiders (family Lycosidae), this behavior appears to be a moderately successful way to survive being grasped by a predator (Klawinski & Formanowicz 1994; Punzo 1997). It is also relatively common, with previous studies indicating that 8–32% of individual wolf spiders collected from natural populations were missing at least one leg (Brueseke et al. 2001; Apontes & Brown 2005).

Most small-bodied wolf spiders are cursorial foragers that do not build prey-capture webs; instead, they rely on short sprint bursts both to obtain prey and avoid capture by predators. Thus, the loss of a leg might be costly to wolf spiders if it reduces running speed. Under some conditions, this cost might be slight or nonexistent. For example, leg autotomy did not affect normal locomotion of female *Pardosa milvina* (Hentz 1844) (Brueseke et al. 2001), nor did it affect prey capture success in laboratory settings for this species (Brueseke et al. 2001), *Schizocosa ocreata* (Hentz 1844) (Amaya et al. 2001; Wrinn & Uetz 2008) or *Trochosa terricola* Thorell 1856 (Amaya et al. 2001). However, the cost of leg loss might be greater in situations in which spiders run at or near their maximum speed, as when confronted by a predator. Decreased maximum running speed following autotomy has been found for male and female *Pirata sedentarius* Montgomery 1904 (Apontes & Brown 2005) and for female *S. ocreata* and *T. terricola* (Amaya et al. 2001), suggesting that these spiders may pay a price for autotomizing a leg.

In this study, we examined the effects of leg autotomy on terrestrial and aquatic burst speed in the wolf spider *Pardosa valens* Barnes 1959. This spider occurs in the cobble zone of small mountain streams of southeastern Arizona, USA, moving easily both on land and on top of the water's surface. Based on prior research, we expected that leg loss would negatively affect terrestrial speed, but no studies of which we are aware have examined the effect of leg autotomy on aquatic speed. We therefore determined maximum sprint speeds of

each sex on both surfaces in order to address two primary questions: Does leg autotomy affect sprint speed on either substrate? And, do males and females differ in sprint speed on either substrate?

METHODS

Collection of study animals.—*Pardosa valens* is a small (30–140 mg) wolf spider found from Arizona and New Mexico south into central Mexico (Barnes 1959). As in many spiders, the sexes are dimorphic in size with females larger than males. At our study site in the Chiricahua Mountains of southeastern Arizona, *P. valens* occurs at an estimated density of 500–700 individuals per 50 m stretch of stream, and leg autotomy is common (25–30% of females and 40–45% of males missing at least one leg; C. Brown, D. Formanowicz & C. Amaya, unpublished data).

We collected adult spiders with all legs intact on 15 June 2005 (24 females, 35 males) and 16 July 2006 (25 females) from the cobble zone along Cave Creek, ~0.7 km NW of the Southwestern Research Station (SWRS), Cochise Co., Arizona (31°52′59.5″N, 109°12′20″W, altitude = 1620 m). We returned all spiders to the laboratory at SWRS and weighed them using an analytical balance (to the nearest 1 mg). Spiders were then housed in the laboratory in 15-ml centrifuge tubes stoppered with a wetted cotton ball and laid horizontally. We did not offer the spiders prey either before or during the subsequent experiments, a period of starvation (4 d) which is likely well within the range experienced in the field (e.g., Nyffeler & Breene 1990). The laboratory was exposed to an ambient light and temperature regime.

Experimental protocol.—On the day following collection, we conducted terrestrial and aquatic sprint speed trials for all intact *P. valens*. For each sex, we randomly assigned half of the individuals to be tested first on the terrestrial track and then on the aquatic track; substrate order was reversed for the remaining individuals. We allowed each spider a minimum recovery time of 6 h between trials.

We conducted terrestrial running trials along a 1 m racetrack. This consisted of a square piece of acrylic tubing (2.5 cm width) glued to a plywood board and marked off in 25 cm intervals. At one end of the race track, we glued a small section of tubing which could be blocked at either end by removable pieces of index card ("gates"); this served as the holding chamber for a spider before a trial began. Spiders were placed individually into this holding chamber and given 15 min to acclimate. One of us (CAB) then removed the gates and, using a square piece of cardboard glued to the end of a glass rod, tapped the spider's rear legs to initiate running. As the spider ran, the glass rod was pushed down the track to prevent the spider from turning around and retreating, and the rear legs were tapped again if the spider stopped. The rod was never used to push the spider. A second person (DRF) measured the time required to run each of the four 25-cm segments using a hand-held stopwatch. A single trial was done for each spider.

The aquatic track was constructed using 10-cm diameter polyvinylchloride (PVC) sewer pipe. A section 1 m in length was halved lengthwise, and a PVC cap was cemented to each end. We then sealed the joint between the pipe and cap using silicone rubber. We marked the floor of the pipe in 10-cm

segments, beginning at the contact point with one cap edge. Tap water was added to a depth of ~3 cm; preliminary trials indicated that spiders ran normally using this source of water. One of us (DRF) began a trial by holding a spider's centrifuge tube at one end of the track, with the open end of the tube ~1 cm above the water's surface, and gently tapping on it to induce the spider to exit. Spiders that ran down the track immediately were not prodded. If the spider did not run, or if it moved backward under the cap, it was gently prodded using the tip of the centrifuge tube or a pair of forceps until it ran in the correct direction or until we were sure it would not run at all (see Results). As in the terrestrial trials, a single run was done for each spider. All aquatic trials were videotaped with a digital camcorder (Sony Handycam model DCR-PC1000). From these recordings, one of us (CAB) recorded the maximum distance traveled by a spider without stopping, and, using a stopwatch, the time required to run this distance.

Following completion of trials using intact spiders, we induced each individual to autotomize a haphazardly-selected leg by grasping the femur of the leg with fine forceps; the leg then autotomized at the coxa-trochanter joint as the spider pulled away (Foelix 1996). This caused a small loss of hemolymph, but the break rapidly sealed and the spider was otherwise unaffected. We then repeated the terrestrial and aquatic running trials two days after legs were autotomized, using the same order of substrate use for each spider as used in the intact trials. Using this experimental procedure, we assume that any physical or psychological stress from autotomy had abated after two days, so that any differences observed in locomotion were due to autotomy alone rather than the stress of the procedure; however, we recognize that this is an untested assumption in our design. After completion of all running trials, spiders were returned to Cave Creek.

Statistical analysis.—For the terrestrial trials, we calculated speed in cm/s by dividing 25 cm by each interval time. For each spider, we used the maximum speed over a single 25 cm interval in our analyses (using other measures, such as speed over the entire meter or mean interval speed, gave qualitatively similar results). For the aquatic trials, we calculated speed in cm/s by dividing the maximum distance run by the time required to run this distance. In all analyses, sprint speed was natural-log transformed to reduce variance heterogeneity.

We analyzed the 2005 sprint speed data using two-factor repeated measures ANOVAs (RM-ANOVA), with sex (male or female) and trial order (aquatic first or terrestrial first) as fixed main effects, and leg loss (all legs intact or with one leg autotomized) as the repeated measure. For the 2006 sprint speed data, where we had only females, we performed one-factor RM-ANOVAs, with trial order as the main effect and leg loss as the repeated measure. Separate RM-ANOVAs were conducted for the aquatic trials and the terrestrial trials in both years. We included trial order as a main effect, because environmental conditions likely varied between the times when trials were conducted. For example, temperatures in the laboratory were higher in the afternoon or early evening trials (30–31.5°C) than they were in the morning trials (25–27.5°C), and temperature is known to affect sprint speed in ectotherms (e.g., Lailvaux 2007).

We also used a two-factor RM-ANOVA to analyze the distance run (in cm) during aquatic trials in 2005; again, main effects were sex and trial order, and leg loss was the repeated

Table 1.—Terrestrial sprint speed in the wolf spider *Pardosa valens* across two years; ANOVA results showing the effects of sex (male or female), trial time (morning or afternoon/evening), and leg status (all legs intact or one leg autotomized). Females were only measured in 2006, and thus sex was not included in the analysis. For 2005, degrees of freedom (*df*) = 1, 45 for all tests. For 2006, *df* = 1, 20 for all tests.

Year	Factor	F	P
2005	Sex (S)	0.04	0.84
	Trial Time (T)	11.98	0.001
	Leg Status (L)	13.36	0.001
	S × T	5.56	0.023
	S × L	0.19	0.66
	T × L	0.32	0.58
	S × T × L	0.07	0.79
2006	Trial Time	2.51	0.13
	Leg Status	0.87	0.36
	T × L	0.41	0.53

measure. Propensity to run in the 2005 aquatic trials was analyzed using log-linear models, with sex, trial time, and leg status (intact/autotomized) as main effects.

Finally, we compared female sprint speeds between the two years using two-factor ANOVAs, with year and trial order as fixed main effects. All analyses were performed using Statistica version 4.5 (StatSoft 1993), with $\alpha = 0.05$.

RESULTS

Of the 35 males collected in 2005, 10 would not run in the aquatic trials when intact and were excluded from further analyses. Nine males completed the intact aquatic trials but would not run on water following autotomy; these we included in the terrestrial data analysis but removed from the aquatic data analyses. In addition, three females collected during 2006 laid eggs following capture and were excluded from analyses. Females (90.8 ± 22.2 mg, $\bar{x}$ ± SD) collected in 2005 were significantly heavier than males (44.5 ± 7.4 mg; $F_{1,50} = 144.0$, $P < 0.0001$) collected that year and were also significantly heavier than females collected in 2006 (64.9 ± 19.0 mg; $F_{1,48} = 20.5$, $P < 0.0001$). Despite these differences, including log-transformed mass as a covariate did not qualitatively change any of the results in the following analyses; we therefore do not report results using mass-adjusted speeds.

In the 2005 terrestrial trials, spiders were significantly faster when intact than when missing a leg, and spiders running later in the day were significantly faster than those running earlier in the day (Table 1, Fig. 1A). Spider sex did not affect terrestrial sprint speed, and no interactions were significant.

In the 2005 aquatic trials, females were significantly faster than males (Table 2, Fig. 1B). Spiders were again significantly faster when intact than following autotomy, but this effect differed between sexes; female sprint speed declined significantly after autotomy, while male speed did not (Table 2, Fig. 1B). Although there was no significant main effect of trial order, there was a significant interaction between trial order and leg loss. Autotomized speeds were similar to intact speeds for spiders that were run in aquatic trials early in the day, but autotomized speeds were substantially lower than intact speeds in trials run later in the day (Table 2, Fig. 1B).

The 2006 trials involving only females exhibited similar trends to the 2005 trials, as sprint speeds decreased following
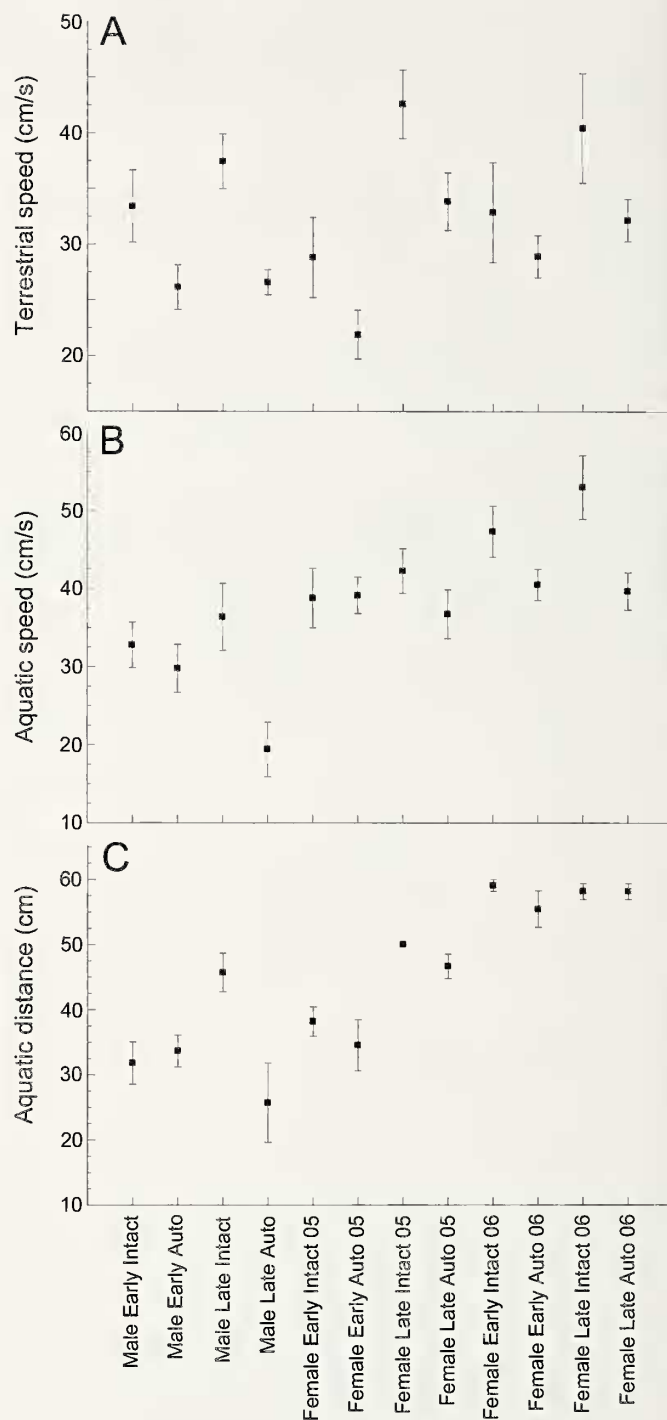

Figure 1.—Mean sprint speeds (±1 SE) on a solid surface (A) and on water (B), and mean distances run on water (C). Early and Late refer to trials run in the morning or the late afternoon/evening, respectively. Intact indicates that all legs were present; Auto indicates that a single leg had been removed. Male data are from 2005 only; females were studied in both 2005 and 2006. In 2005 the distance (C) visible in videos of the aquatic racetrack was 50 cm, while in 2006 the distance visible was 60 cm.

autotomy and increased during trials run later in the day. However, these effects were weaker than in 2005, with only the leg loss treatment in aquatic trials showing statistical significance (Tables 1, 2; Fig. 1A, B). Intact female speeds in

Table 2.—Aquatic sprint speed in the wolf spider *Pardosa valens* across two years; ANOVA results showing the effects of sex (male or female), trial time (morning or afternoon/evening), and leg status (all legs intact or one leg autotomized). Females were only measured in 2006, and thus sex was not included in the analysis. For 2005, degrees of freedom (df) = 1, 37 for all tests. For 2006, df = 1, 20 for all tests.

Year	Factor	F	P
2005	Sex (S)	15.16	0.0004
	Trial Time (T)	1.45	0.23
	Leg Status (L)	10.04	0.003
	S × T	1.91	0.17
	S × L	5.59	0.02
	T × L	9.18	0.004
	S × T × L	2.40	0.13
2006	Trial Time	0.38	0.55
	Leg Status	7.94	0.01
	T × L	0.86	0.37

the aquatic trials and autotomized female speeds in the early terrestrial trials were significantly faster during 2006, while other comparisons between 2005 and 2006 were not significantly different (Table 3; Fig. 1A, B).

During aquatic trials, females ran a significantly longer distance before stopping than did males, and spiders ran significantly farther when intact than following autotomy (Table 4, Fig. 1C). Differences between sexes were most pronounced during trials run early in the day. The propensity to run was significantly affected by sex, as male spiders were less likely to run than were females (log-linear analysis, partial association of the sex by run interaction effect: partial χ^2 = 15.4, df = 1, $P < 0.001$; all other partial associations, $P > 0.15$). In all cases where a spider did not run, it appeared to become trapped in the water's surface film upon exiting the vial.

Spider mass was not correlated with sprint speed on either surface when intact or when missing a leg ($-0.30 < r < 0.24$, all $P > 0.22$). Aquatic and terrestrial sprint speeds were positively correlated in intact males ($r = 0.39$, $P = 0.047$), but were uncorrelated in autotomized males ($r = -0.27$, $P = 0.31$)

Table 3.—Terrestrial (TERR) and aquatic (AQ) sprint speed in females of the wolf spider *Pardosa valens*; ANOVA results showing the effects of year (2005 or 2006) and trial time (morning or afternoon/evening). For terrestrial trials, degrees of freedom (df) = 1, 45 for all tests. For aquatic trials, df = 1, 43 for all tests. For leg status, INT indicates that all legs were intact, and AUTO indicates that one leg was autotomized.

Substrate, leg status	Factor	F	P
TERR, INT	Year (Y)	0.24	0.63
	Trial Time (T)	8.40	0.006
	Y × T	0.44	0.51
TERR, AUTO	Year (Y)	3.21	0.08
	Trial Time (T)	13.13	0.001
	Y × T	4.91	0.03
AQ, INT	Year (Y)	5.82	0.02
	Trial Time (T)	2.01	0.16
	Y × T	0.0004	0.98
AQ, AUTO	Year (Y)	0	1.00
	Trial Time (T)	2.19	0.15
	Y × T	1.44	0.24

Table 4.—Distance moved before stopping in the 2005 aquatic trials for the wolf spider *Pardosa valens*; ANOVA results showing the effects of sex (male or female), trial time (morning or afternoon/evening), and leg status (all legs intact or one leg autotomized). For all tests, df = 1, 37.

Factor	F	P
Sex (S)	12.10	0.001
Trial Time (T)	0.01	0.94
Leg Status (L)	18.03	0.0001
S × T	5.30	0.027
S × L	0.13	0.72
T × L	2.95	0.09
S × T × L	17.43	0.0002

and in females during 2005 (intact: $r = 0.12$, $P = 0.56$; autotomized: $r = 0.16$, $P = 0.48$) and 2006 (intact: $r = -0.08$, $P = 0.74$; autotomized: $r = 0.36$, $P = 0.10$).

DISCUSSION

Our results indicate that the loss of a leg negatively affects sprint speed in the wolf spider *Pardosa valens*, but the strength of this effect varies with substrate, sex, and trial order. Looking first at the terrestrial trials, both sexes were significantly slower following leg autotomy during 2005, while in 2006 female speed following autotomy declined but was not significantly different from intact speed. These results generally support the hypothesis that leg loss is costly to terrestrial locomotion, as seen in other wolf spiders (Amaya et al. 2001; Apontes & Brown 2005) and other arthropods (e.g., Carlberg 1994; Guffey 1999; Bateman & Fleming 2005; Fleming & Bateman 2007). However, this cost may be most apparent at faster (sprinting) speeds, such as measured here, rather than slower (walking) speeds (e.g., Brueseke et al. 2001). In spiders, and perhaps other arthropods, decreases in high-speed locomotion following autotomy may result from a change in running behavior. Spider leg movements follow an alternating tetrapod gait at normal walking speeds, with matching legs on either side of the body moving asynchronously, and with their movement resembling an inverted pendulum (Foelix 1996; Moya-Laraño et al. 2008). As movement speed increases, biomechanical traits such as stepping frequency and duty factor change (e.g., Ward & Humphreys 1981; Spagna 2006), which can cause legs to move either more (Ward & Humphreys 1981) or less (Foelix 1996) asynchronously. The loss of a leg could thus make it more difficult for a spider to switch efficiently from low-speed to high-speed mechanics, resulting in decreased speed.

In the aquatic trials, males ran significantly slower following leg autotomy, while female speed decreased significantly only in 2006. This represents the first evidence that leg loss can negatively affect aquatic surface locomotion in a spider, which again may result from a biomechanical change in the way spiders move on the water's surface. Aquatic locomotion occurs in at least six families of spiders, but is most common in the Pisauridae (fishing spiders) and Lycosidae (wolf spiders) (Stratton et al. 2004). Many fishing spiders and wolf spiders, including *P. valens*, use a rowing or galloping motion when on the water's surface, which involves synchronous movements of pairs of legs on either side of the body (Stratton et al. 2004). Autotomy may decrease the efficiency of these motions, for

example by lowering the torque produced by the power stroke on the side of the body missing the leg.

Females were heavier in 2005 than in 2006, and this difference in mass may reflect variation in several traits that could influence how autotomy affects locomotion. First, greater mass could indicate that females collected in 2005 were overall larger in structural size, specifically in leg length, which would have enabled them to attain longer stride lengths and perhaps faster speeds. Although we did not directly measure structural size, we suggest that this interpretation of the size variation is not supported, since it predicts that females would be faster in 2005; instead, we found the opposite to be true. In addition, mass and leg length are not strongly correlated in other wolf spider species (C. A. Brown unpublished data), and neither mass (Apontes & Brown 2005; this study) nor leg length (Apontes & Brown 2005) appears to be strongly correlated with terrestrial sprint speed in wolf spiders (but see Moya-Laraño et al. 2008 for a counter-example in a cobweb spider). Thus, even if females were structurally larger in the 2005 sample, the larger size did not lead to an increase in speed.

An alternative, and perhaps more likely, explanation is that female mass differed between the two years due to differences in body condition that arise from the timing of collection of spiders. Females in 2005 were collected in mid-June, when nearly all were gravid with their first (or, less likely, second) clutch of eggs, while females during 2006 were collected in mid-July, when they were either gravid with a second (or third) clutch or had already oviposited. Since clutch size and mass decline with each successive egg sac produced in wolf spiders (e.g., Brown et al. 2003), 2006 females would be expected to be lighter than those from 2005. On the water's surface, being heavier may be detrimental if this increases the area of contact with the water and thus increases drag. This idea draws support from the fact that lighter 2006 females were significantly faster than heavier 2005 females when all legs were present, and thus suffered a more precipitous decline in speed following autotomy (when speeds were more similar). On land, heavier spiders may be less able to compensate for leg loss than lighter spiders, due to a decreased ability to generate the force necessary to move the spider through the inverted pendulum motion (Moya-Laraño et al. 2008); this is suggested by the greater decrease in speed of autotomized spiders during the early trials in 2006.

Male *P. valens* were significantly slower than females on the water's surface, but not on land. This latter result was surprising, given that male wolf spiders are generally smaller than females in overall body size and leg length, although males may have longer legs for a given body size (e.g., Apontes & Brown 2005). It also contrasts with results for the wolf spider *Pirata sedentarius*, the only other study comparing male and female terrestrial sprint speeds, in which females are significantly faster (Apontes & Brown 2005). Body mass (perhaps reflecting reproductive status) may have affected our results, with heavier (probably gravid) females having terrestrial speeds more similar to males than they would if lighter (post-oviposition). However, we would expect the same pattern to hold during aquatic locomotion, since additional weight appears to lower female speed on water more than on land. Since this was not the case in our study, we remain unsure about the cause of the differences in the relationship of male to female speed between the two substrates.

In addition to running more slowly on water, males were less likely to run than females and, when they did run, ran shorter distances than females before stopping. All cases in which the male did not run exhibited a similar pattern: upon exiting the tube, the male appeared to become wetted and stuck in the surface tension of the water; if prodded, the male would then turn slowly in a circle moving just one or a few legs. In addition, all males that did this in their initial attempt on the aquatic track repeated the behavior when we informally attempted a second time to induce them to run. Based on our field observations, this was an unexpected behavior in *P. valens*. We have observed numerous instances of both male and female spiders moving across the water to avoid capture, and have never seen one become entangled in the surface tension as occurred in these trials. Although this may have been due to differences between the tap water used and natural stream water (e.g., presence of planktonic algae in the latter), we think it unlikely that the tap water strongly affected the ability to run, as the majority of males and all females were capable of running on the surface when all legs were intact. A more intriguing possibility is that males differ from each other, and from females, in their ability to prevent capillary adhesion of water, either through differences in cuticular composition or in the density or composition of hairs (Suter et al. 2004). If so, we would predict that males with less ability to prevent adhesion of water should be less likely to be found near water and less likely to attempt aquatic locomotion.

Females ran faster in the later (afternoon/early evening) terrestrial trials than in the earlier (morning) trials, although this time of day effect was significant only in the 2005 trials. For males and for aquatic locomotion, speeds were also generally higher in the later trials, although the differences were small and not significant. Thus, our results suggest that the timing of the trials has some influence on running speed, more so for females and for terrestrial locomotion. Several environmental variables, such as light level, temperature, and relative humidity, may have differed between the two trial periods and thus affected sprint speeds. Temperature in particular is known to affect many physiological processes and behaviors, and room temperatures were on average 4–5°C warmer during the trials performed later in the day. Although little research exists on the influence of temperature on spider locomotion, it would not be surprising for sprint speeds to be positively related to temperature in this group. Locomotory performance is known to increase with temperature in other ectotherms (e.g., reptiles: Lailvaux 2007), and, in spiders, temperature is known to positively influence life history characteristics such as reproductive output and developmental rate (Li and Jackson 1996).

In summary, we find that leg autotomy in the wolf spider *Pardosa valens*, although of obvious benefit for immediate survival in the face of a predatory attack, induces potential costs to future survival in the form of decreased sprint speed both on land and on the water's surface. However, the relative strength of these costs depends on aspects of both the spider (its sex and perhaps its size or reproductive status) and the environment (the substrate, temperature of the air and/or substrate). Since all life stages of *P. valens*, whether intact or

missing legs, are active throughout the day on both surfaces, each of these factors may be an important influence on future survival; future studies which focus on each factor separately should allow us to better understand the relative importance of each.

ACKNOWLEDGMENTS

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